TWENTY-FIVE YEARS OF MIGRATION OF THE PAINTED LADY BUTTERFLY, VANESSA CARDUI, IN SOUTHERN CALIFORNIA[1]

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The British naturalist, C. B. Williams, has for some years been collecting information from correspondents all over the world relating to migratory species of butterflies. In addition, he has made numerous observations of his own in various parts of the world (Williams, 1930; Williams et al, 1942). Yet little seems to have been done to concentrate on a single migratory species in a single region. The studies of Woodbury, Sugden, and Gillette in Utah (Woodbury et al, 1942; Sugden, et al, 1947) and of Beall in Ontario, Canada (1941) are important exceptions.

The author, who is not an entomologist, but who is interested in migration problems from the standpoint of animal ecology, first came in contact with the migration of the painted lady butterfly, *Vanessa* (*Pyrameis*) *cardui,* in the spring of 1924, in what appears to have been the greatest migration of the species since 1901. As a newcomer in southern California, he did not realize that such a migration was an exceptional phenomenon, in spite of the numerous questions which were asked him about it. It was not until the spring of 1925, when during the entire spring he saw only two painted ladies, and when he found that the literature was almost entirely lacking in reports of the 1924 migration, that he realized that here was an ecological problem of a spectacular nature which was being almost entirely neglected. As Redlands is popularly supposed to be strategically located on the migratory routes of birds, it promised to be a favorable location for analyzing butterfly migration.

Since that time there have been three migration years, 1926, 1941, and 1945, none of them involving as large numbers as 1924, but all conspicuous and lasting for several weeks. The plan of analysis has been to organize observers in all parts of southern California for making simultaneous observations and reports. The fact of one interval of fifteen years between migrations shows the difficulty of much organizing in advance (Abbott, 1941, 1946).

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This plan of study has involved in general two parts: detailed records at the University of Redlands with the assistance of students in zoology classes; and reports from other regions in southern California. In 1926 and 1941, I wrote to individuals whom I knew, mostly former students, in locations from which I desired information. In 1945, through lack of time to make contacts by correspondence, I advertised the matter in the press, and this proved to be the most fruitful in results. Of the many volunteer contributors, I wish to mention in particular Mr. Roy Cain of San Bernardino, who, with an occupation making him travel to all parts of San Bernardino County, kept detailed daily records for the entire period of the migration, approaching two months.

The study is a long way from solving any fundamental problems of insect migration. But it has established a few facts which are at least the basis for further work.

In the following summary, migration is used for any mass movement of animals from one locality to another, without assuming any theory as to its cause. Butterflies refers to the species *Vanessa cardui* unless otherwise specified.

Duration in Time

A migration extends over a considerable period of time, approaching two months. The 1924 and 1926 migrations were from early February to late March; the 1941 and 1945 migrations were from early March to late April. Most of the printed accounts, such as those of California observers summarized by Williams, deal only with a few days at the height of the migration.

The beginning of a migration can be noted by observing that the butterflies are all flying in the same direction, each one in a straight line. When ten butterflies are seen crossing a city street at the same angle in a distance of half a mile, it is time to open a notebook.

Each year's migration consists of a series of waves, the numbers increasing more or less daily to a maximum, then diminishing and increasing again. In 1926 and 1941 there were thus three peaks of maximum abundance at scattered intervals. In 1945 there were apparently three peaks within two weeks, so close together as to make separation somewhat uncertain. The relation of the waves to weather conditions is discussed later in this paper.

GEOGRAPHICAL EXTENT

The geographical extent should be considered in relation to the map of southern California (figure 1). It appeared to vary slightly in the different years, yet this variation may have been due to incompleteness of reports from certain regions. The 1941 records show best the complete path of migration from Campo on

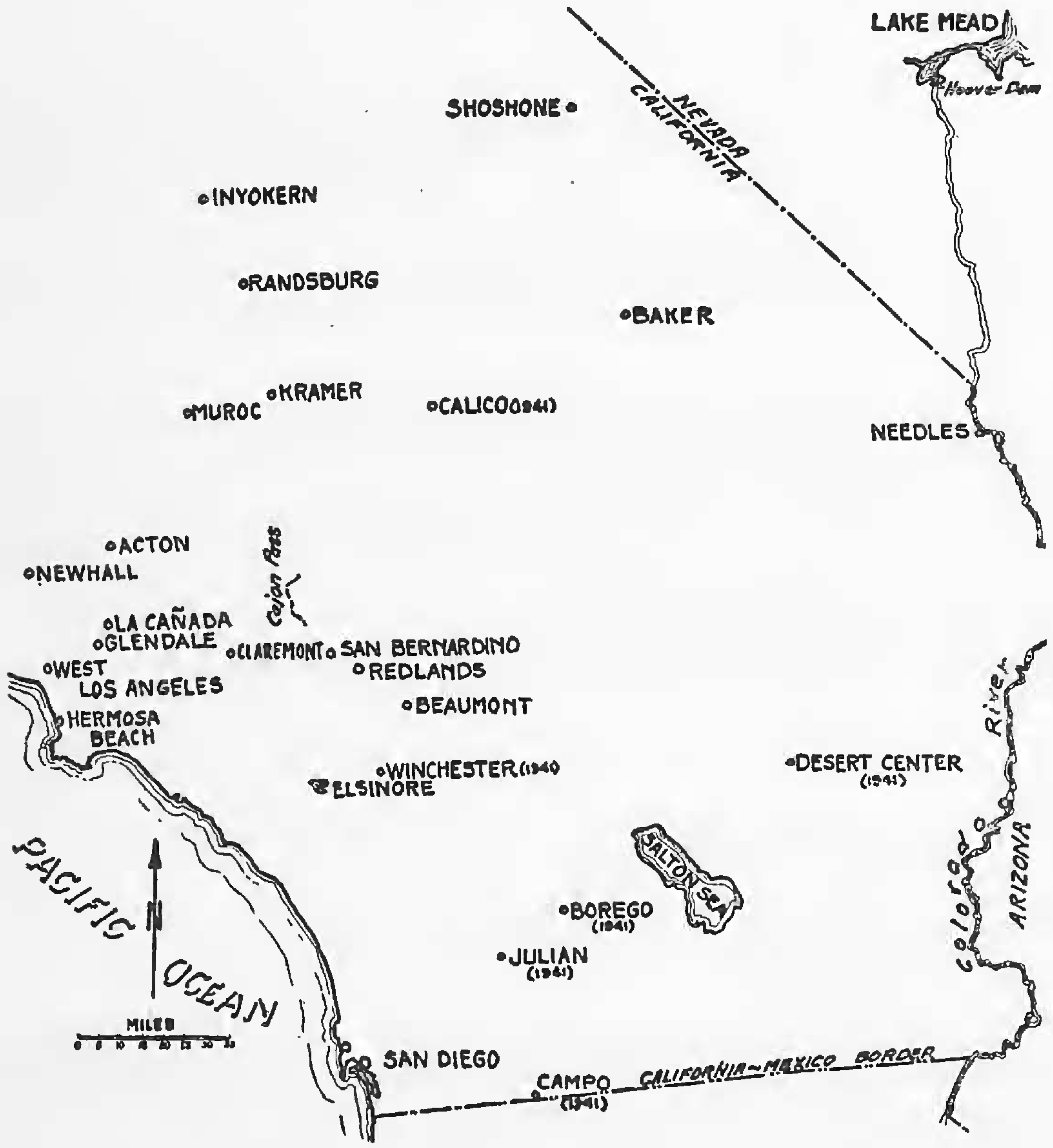

Figure 1. Map of Southern California, showing the principal localities referred to. Migrants were reported from all these points in 1945, except those marked 1941. Cajon Pass is the principal pass through the mountain ranges to the Mohave Desert on the north. South of it is the interior valley and coast region of Southern California. Between Borego and the Colorado River is the Colorado Desert. (Drawn by D. L. Soltau.)

the Mexican border north to the southern slope of the San Bernardino Mountains in the vicinity of Cajon Pass. There they appeared to be crossing the east-west range without taking advantage of the pass. Intermittent observations north of the mountains followed them to Calico in the Mohave Desert, a distance of 170 miles from Campo.

The country covered south of the mountains was the type of California semi-desert known as brush or chaparral. North of the mountains it was true desert of the high altitude Mohave Desert type.

The eastern border of the migration extended well into the Colorado Desert, which is lower in altitude and hotter than the Mohave and in general a barrier to distribution as the Colorado River is approached. Incomplete records on the western border indicated that the butterflies did not quite reach the ocean beaches that year.

The 1945 records are valuable as showing a cross section of simultaneous migration from Hermosa Beach to Needles on the Colorado River, a distance of 225 miles. Over most of this front the butterflies crossed the mountains from the southern valleys and spread north over the Mohave Desert, reaching a point 225 miles north northwest of Campo. Reports indicated approximately the same peak days over the entire cross section.

As there was no opportunity for records from south of the Mexican border, the point of origin of the flights could not be determined. But in California they covered an area at least 225 by 225 miles. No reports were received of their crossing the mountains further west to Bakersfield in the San Joaquin Valley or to Santa Barbara on the coast.

The figures just given for the extent of the migration do not indicate that butterflies were evenly distributed over the territory at any one time. Counts showed axes of migrating paths, the numbers diminishing toward the boundaries. For example a wave of migration from March 14 to 21, 1941, had its axis in Redlands, with its boundaries approximately eight miles west and eight miles east of Redlands. By March 22 and 23 the axis had shifted a few miles west. W. S. Wright wrote of passing through three migrating paths in 1926 during a sixty mile ride inland from San Diego in an easterly direction, the butterflies being absent in the intervening regions.

DIRECTION OF MIGRATION

The direction of migration throughout the territory was usually north-northwest, varying to northwest or north. This in general was directly against the prevailing wind. Yet there were enough exceptions to suggest that butterflies can fly as efficiently at right angles to the wind as directly against it. It may be noted that Woodbury, Sugden, and Gillette (1942), in studying the 1941 migration in Utah and adjacent states, found the direction of flight varying from north to northeast. The territory studied by them is separated from that included in the present paper by a hot dry desert which is an effective barrier to many moisture-requiring species.

The possibility that flights against the wind may be flight toward more favorable moisture conditions is taken up later.

TOPOGRAPHY AND DIRECTION OF FLIGHT

The course and direction of the flight were not determined by natural topographic features. Cajon Pass, San Gorgonio Pass, and the branch of the latter known as San Timoteo Canyon are popularly thought of as migration routes. Yet the butterflies flew in straight lines, crossing these canyons and their branch canyons at any angle, or sometimes missing them entirely.

To maintain their straight path of migration, butterflies regularly rose over obstacles such as hedges and trees, even tall eucalyptus trees and three story buildings, yet they consistently kept within a few feet of the ground otherwise. Each individual butterfly appeared to be maintaining an even distance above the ground. A striking illustration could be seen from the roof of the Hall of Science at the University of Redlands where one looked down on the migrants and observed that when they flew over trees they flew no higher than necessary. When they reached the vertical south wall of the Hall of Science, most of them stopped to feed on a lantana bush, and on leaving flew around the west end of the building before resuming the north-northwest direction. A few, however, ascended in a spiral and passed over the roof.

It was also interesting to watch them cross a narrow canyon with steep walls. They consistently flew down one wall and flew up the opposite wall rather than crossing from rim to rim, which to the observer would have seemed the simpler method of following a straight line.

Rate of Flight

Each butterfly appeared to be flying at a steady even rate, although there were obvious individual differences. Measurements were made of the rate of flight by recording with a stop-watch the time required to pass over a measured distance of ground, the measurements being taken on days when the wind was very slight. The 1941 measurements showed times of between 5 and 10 seconds in flying 100 feet. The average, 7.5+ seconds, gives approximately 6.6 minutes for one mile and 9.1 miles per hour. A similar set of figures, made on the same field in 1945, averaged 7 seconds for 100 feet, 6.16 minutes for one mile, and 9.7 miles per hour.

Time of Day and Weather Conditions

During a migration the largest flights occurred in warm, sunny weather, with a flight ceasing almost entirely if several cold, rainy days came together. This subject needs further investigation as a factor in the varying curve of abundance during the entire migration period.

The best statistical record of the hours of daily flight was kept at Redlands by M. Salmond, March 20 to 27, 1941. On all of these days the flight began between 8:15 and 9:00 a.m., and ended between 3:20 and 5:15 p.m. This was during a period when there was fog from late afternoon to early morning.

The actual beginning of a daily flight was described by Miss Salmond on April 25, 1941, when, at 6:50 a.m. six butterflies, which apparently had been "sleeping" on the lawn, flew up, circled around more or less, and flew off to the northwest.

Feeding

Butterflies stopped freely to feed. Favored food plants were lantana, apricot, greasewood (*Adenostoma fasciculatum*), pussy-willow, various flowers of park and campus.

Other Species

Were other species associated with *Vanessa cardui* in the migration? It is difficult to give an absolute answer, because the common species *Vanessa caryae*, usually considered non-migratory, remembles *cardui* so closely that they look alike when flying. However, it is easy to identify the two species when they are feeding on a lantana bush. The author did this many times, and, while both species fed together, only individuals of *V. cardui* were seen to arrive from the southeast and leave in a northwest direction. The *V. caryae* left in any direction, usually flying to other plants.

Occasionally single individuals of *Vanessa atalanta*, easily distinguished, were seen in a migratory swarm of *V. cardui*, and these also fed commonly on the same food plants. It was noted, however, that the individuals of *V. atalanta* stayed longer on a food plant, and not once was one seen to fly away from it in a definite direction. Therefore the present conclusion limits the migration to the one species.

DISCUSSION

The migration of *V. cardui* is spectacular, always in the same direction with minor variations, at very irregular intervals, and through country where the climatic and vegetation types change very slightly. There is no present evidence that any of the migrants return, and they do not increase the permanent population of the territory over which they pass.

The two questions which most commonly occur are:

(1) Why do they migrate?

(2) What determines the direction of migration?

The most commonly proposed theory for the cause of this type of migration is the "pressure of population theory." This has been applied to migrations of insects, mammals, and even the rhythmic migration of birds.

Chapman, in his paper "Insect population problems in relation to insect outbreak" (1939), shows in detail how this theory holds true for insects under the most complex combinations of conditions. He includes migration as one of the manifestations of an insect outbreak.

To quote the part directly applicable to *V. cardui:*

"In cases represented by insects having a high biotic potential, the relaxation of environmental resistance during a single generation, or even for a very short time during a critical part of the reproductive period, may result in a population increase of outbreak proportions. On the other hand, in case of a low biotic potential or a slight relaxation of environmental resistance, it may be necessary to have several successive periods of reduced resistance occur to make it possible for a population to build itself to outbreak proportions."

Without knowing how Chapman would characterize the biotic potential of *V. cardui,* the paragraph just quoted gives enough variables to account for the irregular intervals between migrations and for the variation in numbers in the different years. Chapman further states:

"In the case of migrating insects, it is necessary to study the area from which they migrate to determine whether conditions are such that populations will be built up and that the breeding conditions will encourage the populations to migrate."

Because it is not known how far south of the Mexican border the flights originate, it is uncertain whether it is chiefly in desert or semi-desert conditions. But it is known that on the edge of the Colorado Desert in California, during the wildflower season, the corresponding period of maximum insect abundance is in March and April. The variable is the amount of winter rainfall and to some extent its monthly distribution, which has a direct effect on the abundance of wildflowers. A favorable year might greatly increase the butterfly population in the succeeding year. This is a point on which the data are not available.

A report of a concentration of a butterfly population in this region was given to the author by W. S. Wright of the Natural History Museum, San Diego, under the date of April 16, 1926. To quote:

"Early this spring one of our collectors visited the desert near Yuma, Arizona, and on his return reported millions of painted ladies on the desert, feeding on the Desert Encelia. Later a visitor to the museum corroborated this report, adding that the numbers were equally great in the region about Salton Sea and as far west as the entrance to Carriso Gorge on the S. D. and A. R. R. Just prior to the first flight observed in the city, there occurred a strong wind blowing off the desert. Now my theory is that the insects breed on the desert or in contiguous territory and that the strong drying winds cause them to seek other fields. Some instinct, or the force of the wind, drives them westward until they reach the cool ocean breeze, having the effect of turning them from the westward course towards the northeast in this locality."

Is there a possible truth in these sentences that this butterfly is precisely adjusted to an optimum condition of humidity, or of humidity and temperature combined? Does the prevailing north-northwest direction of flight, which exists everywhere except perhaps in the extreme south region described by Wright, represent a direction which maintains this optimum?

If this theory should be correct, it does not explain why they continue on into the Mohave Desert, where the air becomes dry again. It may be that the flight gradually slows down in the Mohave Desert on that account. But it does show the need for experiments on the reaction of this species to moisture and temperature gradients.

Temperature is suggested, because the interior valleys of California and the coastal regions have fewer extremes than the desert. Also the experiments of Kendeigh (1934) on birds indicate that temperature is more important than length of day in determining the fact and direction of bird migration. This is important in the west-east bird migrations in California in which temperature differences are conspicuous and the length of day factor is eliminated.

ADDITIONAL POINTS IN NEED OF STUDY

(1) Do these butterflies lay eggs along the migratory route and do they continue migration after egg-laying? References to egg-laying on migration are made by Woodbury et al (1942) and brief references by Campbell (1924) and Dow (1924); but little evidence is available on this point.

(2) Does a second generation move northward in late summer? Woodbury et al (1924) report one instance in 1935; and W. Hovanitz wrote me on September 18, 1944, that he remembered a single instance in Pasadena, California, in the fall of 1940, but that he had no notes on it. It may be noted that the California tortoise-shell, *Nymphalis californica* Bdv., aggregates and migrates irregularly in the late summer in northern California, but the direction of migration varies from north, through west and south, to southeast (Comstock, 1927; Williams, 1930).

(3) There are no reports of a fall migration of *V. cardui* in California. In 1941, I wrote to all observers who had reported on the spring migration asking them to report on any possible instance of a fall migration. All replies received were in the negative.

(4) A study of the distribution and abundance of *V. cardui* in southern California in a non-migratory year is very desirable, as well as of its behavior reactions.

SUMMARY

(1) The painted lady butterfly, *Vanessa cardui,* has had four migrations in southern California in twenty-five years, in the springs of 1924, 1926, 1941, and 1945.

(2) Against the background of the great migration of 1924, the lesser succeeding migrations have been analyzed qualitatively and to some extent quantitatively.

(3) Time relations. Each migration period lasted nearly two months, showing a succession of increases and decreases with three maxima. The maxima, which were irregularly distributed, appeared to be related to weather conditions. Flying occurred during the sunny hours of the day, and almost ceased during cold, rainy periods.

(4) Geographical extent. This was partially determined by compiling the reports of cooperating observers scattered over southern California. The territory covered in 1941 and 1945, carefully mapped, showed a northward flight from the Mexican border to the leading towns and highways of the Mohave Desert, a distance of 225 miles. This actually is too small a figure, because the flight, or part of it, originated south of the Mexican border, and it may have gone farther north into the less accessible parts of the desert.

(5) Geographical extent, continued. A west-east cross section in 1945 showed butterflies migrating simultaneously in all of the territory from the coast to Needles on the Colorado River, a distance of 225 miles. Farther south, the cross section is narrower, being limited on the east by the driest section of the Colorado Desert. Farther east, in Arizona and Utah, another set of butterflies was in migration, but averaging a month later, in both 1941, and to a lesser degree in 1945 (Woodbury et al, 1942; Sugden et al, 1947).

(6) Most of the territory in which the migration was studied is the California type of semi-desert known as brush or chaparral, although the flights actually extended many miles into the Mohave Desert.

(7) The butterflies fly in a straight line, usually north-northwest, regardless of topography, keeping a few feet above the ground, and rising over obstacles. The flight is usually against the wind, but is just as controlled when the wind comes from a different direction.

(8) The type of migration, large numbers at irregular intervals, is typical of the migrations of those insects and mammals which make a non-returning migration in a predictable direction at irregular intervals. Chapman's application of the "pressure of population" theory is shown to apply to this migration, and is given as the only current hypothesis.

(9) It is suggested, as a hypothesis for further analysis, that, while the direction of wind may not be the factor determining the direction of flight, the effect of the wind on either temperature or humidity may be a controlling factor. If so, the butterflies must be capable of very precise adjustment to these factors.

Acknowledgments

Thanks are due to the many observers, here unnamed, who contributed much of the data on which this study is based; also to D. L. Soltau for the map in Figure 1.

Literature Cited

Abbott, C. H.

1941. The 1941 migration of the painted lady butterfly (*Vanessa cardui*) in Southern California. Bull. Ecol. Soc. Amer. 22:13.

1946. Mapping of the 1945 migration of *Vanessa cardui* in Southern California. Bull Ecol. Soc. Amer. 27.

Beall, G.

1941. The monarch butterfly, *Danaus archippus* Fab. I. General observations in Southern Ontario. II. The movement in Southern Ontario. Canadian Field Naturalist 55(8): 123-129; (9): 133-137, 5 text figs., 1 table.

Campbell, R. E.

1924. Painted lady butterfly. Insect Pest Survey Bull. (Washington) 4: 70-71.

Chapman, R. N.

1939. Insect population problems in relation to insect outbreak. Ecological Monographs (Duke Univ. Press) 9(3): 261-269.

Comstock, J. A.

1927. Butterflies of California. 334 pp., 92 text figs., 63 col, pls. Los Angeles, published by the author.

Dow, R. P.

1924. Migration of Pyrameis cardui. Jour. New York Ent. Soc. 32(3): 121.

Kendeigh, S. C.

1934. The role of environment in the life of birds. Ecol. Mon. 4(3): 299-417.

Sudgen, J. W., Woodbury, A. M., and Gillitte, C.

1947. Notes on migrations of the painted lady butterfly in 1945. Pan-Pac. Ent. 23(2): 79-83.

WILLIAMS, C. B.
1930. The migration of butterflies. xi+473 pp. Edinburgh, Oliver and Boyd.

WILLIAMS, C. B., COCKBILL, G. F., GIBBS, M. E. and DOWNES, J. A.
1942. Studies in the migration of Lepidoptera. Trans. Roy. Ent. Soc. London 92 (1): 101-283; 60 figs., 37 tables, 2 pls.

WOODBURY, A. M., SUGDEN, J. W., and GILLETTE, C.
1942. Notes on migrations of the painted lady butterfly in 1941. Pan-Pac. Ent. 18(4): 165-176, 1 fig.

BOOK REVIEW

The Insect World of J. Henri Fabre. By Edwin Way Teale. Dodd, Mead & Company, N. Y., xvi + 333. 1949. Price $3.50.

Fabre's careful observations and masterful reporting of natural phenomena are too well known to require examination here. The studies which this great French naturalist gave to the world have already been translated into many other languages from the original French. Teale has concerned himself with the English translations of A. T. de Mattos which have long been a source of enjoyment to both naturalists and laymen. By a process of careful editing he has presented 40 interesting excerpts from 13 of the de Mattos books.

These selections are in the identical phraseology of the de Mattos translations but are seldom complete. In order to give a maximum coverage, Teale has done a skillful piece of editing which is worthy of some explanation. For example, Teale will give one paragraph from de Mattos, skip several pages, then present several complete pages without any apparent lack of continuity. In this manner many of Fabre's statements expressing his anti-selectionist views or comments concerning the wonders of divine creation have been deleted. For the younger naturalist these omissions will serve to emphasize the natural wonders of Fabre's world. However, as Teale has indicated in his introduction, an understanding of Fabre's belief in the immutability of creation is necessary for a full appreciation of his abilities and limitations. For the benefit of the reader, Teale has given a brief foreword to each chapter along with the source of each selection. However, chapter ten is credited to the Mason Bees while it should have been referred to chapter six of Bramble-Bees and Others.

Unfortunately Teale did not see fit to illustrate this book, other than with a series of end plate photographs. One of these illustrations is misnamed as a Meloe oil-beetle while it appears to be a member of the genus *Epicauta*.

Minor criticisms as these are no indictment of the excellence of Teale's work in bringing together so many carefully selected and well edited passages from Fabre's life work. This is particularly so since so many of Fabre's observations were the first of their kind and in many cases have not yet been duplicated.—J. W. MACSWAIN.